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Geographic variation in the frog genus *Vanzolinius* (Anura: Leptodactylidae)

W. Ronald Heyer

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—*Vanzolinius discodactylus,* a forest-dwelling frog species of western Amazonia in South America, varies in characters of color pattern, morphology, and advertisement call. Analysis of this variation indicates that very local (site) differentiation results in mosaic patterns of differentiation, largely obfuscating larger geographic patterns. Comparison of available genetic estimates of differentiation for *V. discodactylus* are consistent with the morphologically and advertisement call-based conclusions. A previously studied forest-dwelling lizard and another forest-dwelling frog also demonstrate local differentiation patterns suggesting that the variation in *V. discodactylus* may represent a general pattern for forest-dwelling amphibians and reptiles in Amazonia.

During examination of specimens for a study of *Leptodactylus* species (Heyer 1994), several *Vanzolinius* specimens were encountered. Dr. Claude Gascon found *Vanzolinius* to be relatively common along the Rio Juruá in Brazil and used the species to test the riverine barrier hypothesis (Gascon et al. 1996). A cursory examination of these additional materials suggested that there was considerable variation, which might profitably be studied. The purpose of this paper is to analyze geographic variation in *Vanzolinius.*

Materials and Methods

As many adults, larvae, and recordings of advertisement calls as possible were assembled from major museum collections (Appendix 1).

The sex of individuals was determined either by examination of vocal slits, or dissection to examine gonads. The following categories are used: adult male—vocal slits present; juvenile male—testes present, but vocal slits not broken through; adult female—oviduct folded at least in part; juvenile female—ovaries present, but oviduct straight; juvenile—condition of gonads indeterminate (in some cases, gonads had been removed by previous workers).

Analyses differ depending on the type of data gathered for the characters examined. The following descriptions of characters are arranged by analytical groups.

Color patterns and external morphological features of adult form individuals.—These qualitative traits are categories recorded as either binary or multistate characters. For the latter, states were added to the series as they were encountered during the data-taking phase. The states within each series have no intended or implied relationships or transformation series. Intermediate conditions between states were recorded with the first letter of the state that most nearly approached the condition observed in the specimen examined.

Dorsal snout pattern: Three basic states were encountered: a relatively uniform dark pattern (Fig. 1A); a variegated pattern (Fig. 1B); and a uniform light pattern (Fig. 1C).

Light postorbital eye stripe: A series of symbols define the distinctiveness of the postorbital eye stripes: − [absent]; (+) [indistinct]; + [distinct]; +! [sharply defined].

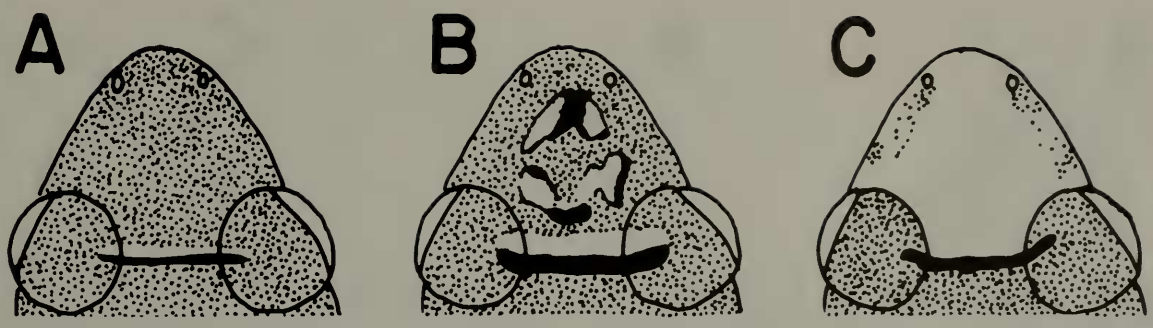

Fig. 1. Dorsal snout pattern standards.

In cases where the two sides of the head differed, both conditions were recorded.

Light subocular bar: The distinctiveness of the bar was noted by the same symbols as for the previous character, except the +! category was not encountered.

Dorsal pattern: Dorsal pattern variation forms a continuum among the more distinctive states recorded. The states recognized are: State A—either an uniform dorsum (brown or tan) or indeterminately blotched (Fig. 2A); State B—the dorsum with very distinct dark markings in the interorbital and interscapular areas (Fig. 2B); State C—distinct interorbital blotch, well defined chevron markings anteriorly and blotches posteriorly on the body (Fig. 2C); State C-1—as previous state except chevrons continuous; State D—a distinct darker straight edged band extending from behind eyes on full extent of dorsum (Fig. 2D); State D-1—as previous state, except sides irregular.

Dark mid-dorsal pin stripe: An interrupted dark mid-dorsal pin stripe was recorded as either present or absent.

Throat and chest pattern.—Variation in this character is continuous among the states encountered: State A—variegated pattern (Fig. 3A); State A-1—as previous state, but light; State B—uniform light pattern (Fig. 3B); State B-1—as previous state, but lateral portions darker; State C—dark speckled pattern (Fig. 3C); State C-1—as previous state, but dark spotting more extensive; State D—dark pattern (Fig. 3D); State E—dark pattern with light spots (Fig. 3E).

Belly pattern: Variation in this character is continuous among the states encountered:

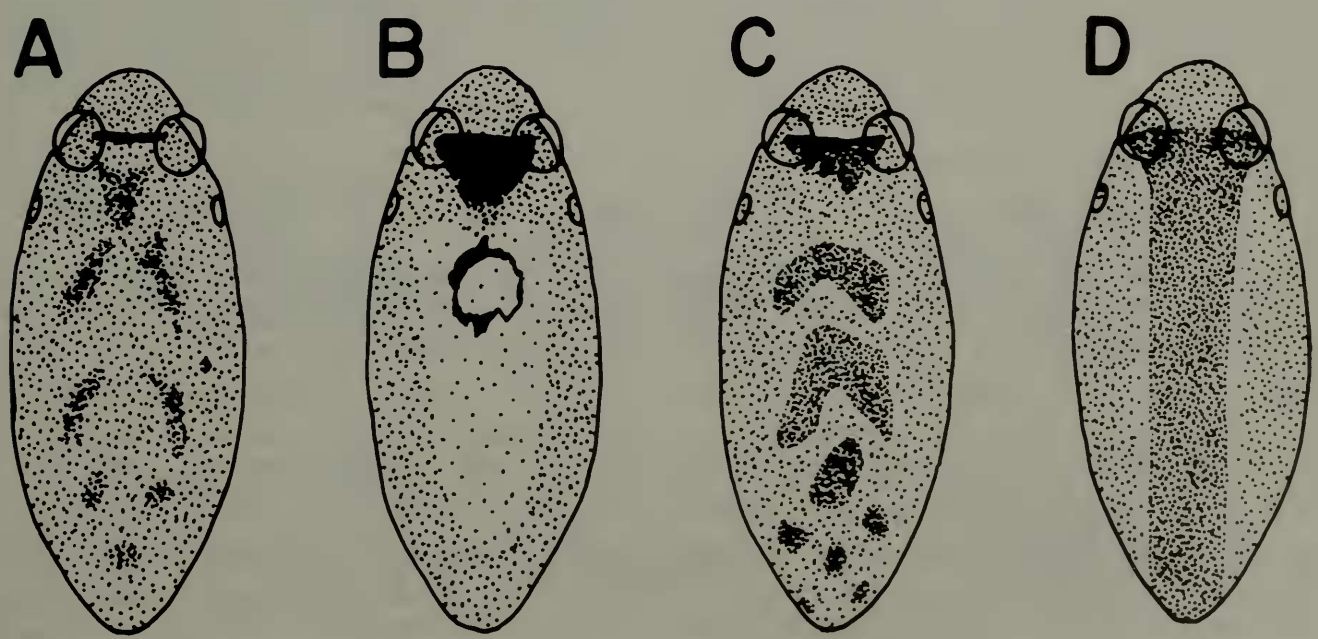

Fig. 2. Dorsal pattern standards.

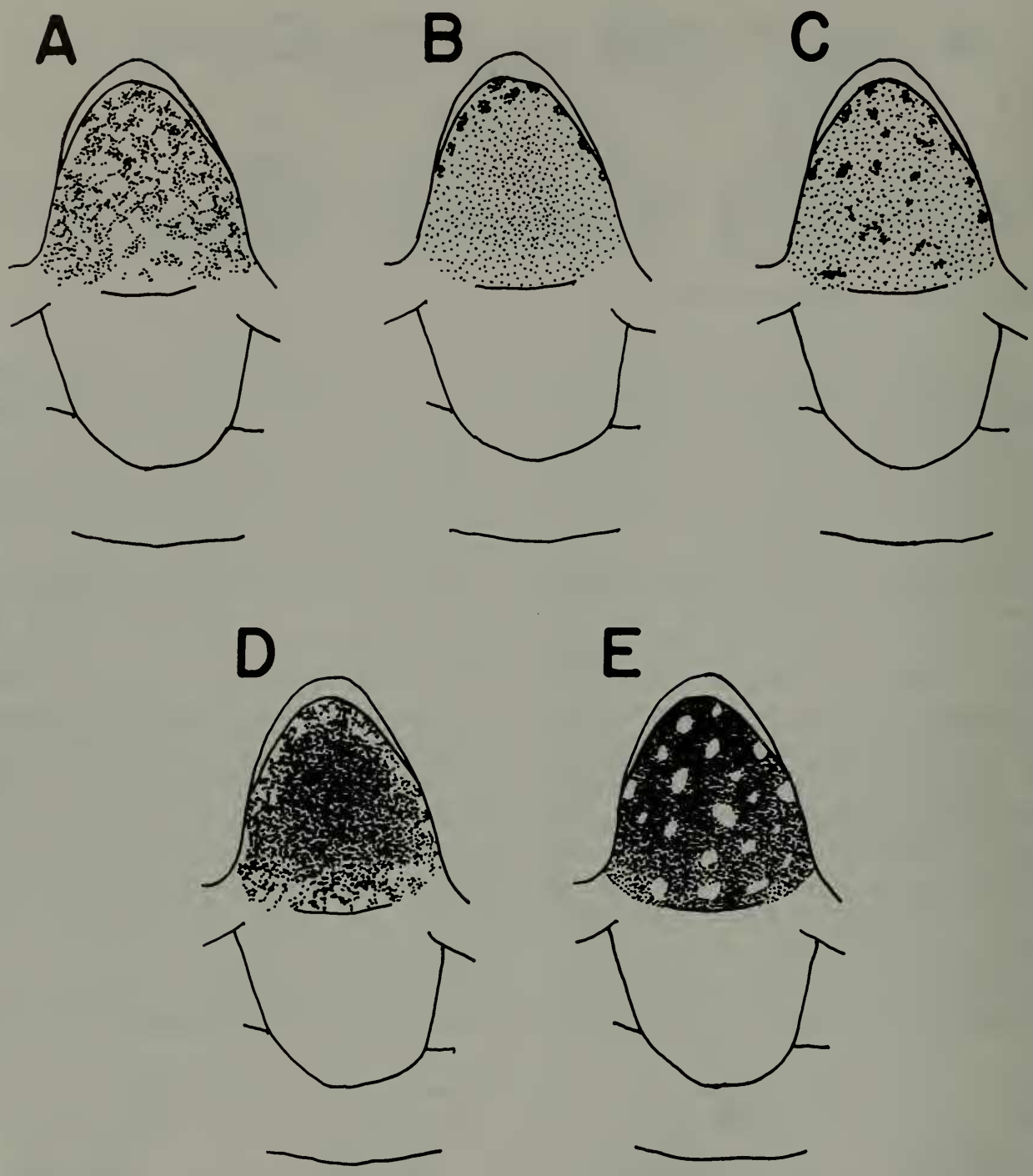

Fig. 3. Throat and chest pattern standards.

State A—speckled pattern (Fig. 4A); State A-1—almost uniform cream pattern; State B—indistinctly mottled, more intense anteriorly (Fig. 4B); State B-1, as previous state, but lighter; State C—distinctly mottled, rather uniform over belly (Fig. 4C); State C-1—as previous state, but lighter; State C-2—as State C but dark anteriorly and no melanophores posteriorly; State D—distinctly variegated dark and light pattern (Fig. 4D).

Posterior thigh pattern: Variation in this character is continuous among the states encountered: State A—indistinctly mottled (Fig. 5A); State B—indistinctly mottled with indistinct dark longitudinal band (Fig. 5B); State C—distinctly mottled (Fig. 5C); State D—speckled with indistinct dark longitudinal band (Fig. 5D); State E—speckled with distinct dark longitudinal band (Fig. 5E); State F—speckled with dark longitudinal band bordered above by light longi-

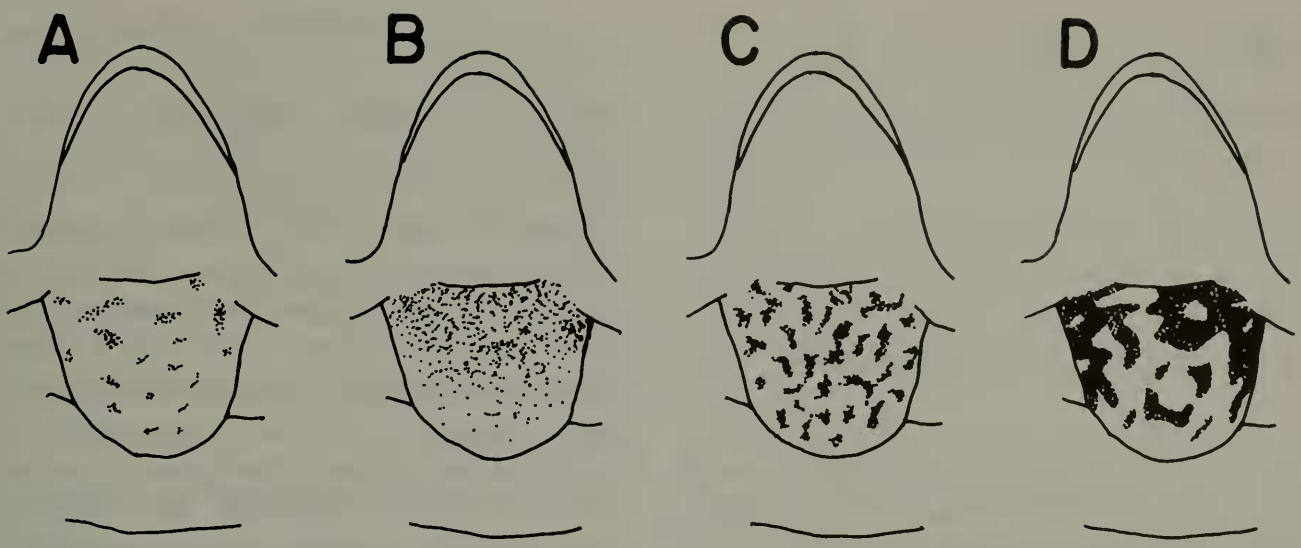

Fig. 4. Belly pattern standards.

tudinal stripe (Fig. 5F); State F!—as for State F except light stripe very distinct.

Outer tarsal pattern: Data were taken on the distinctiveness of the outer tarsal pattern relative to the dorsal tarsal pattern. However, variation turned out to be minimal and scoring could not be done consistently. These data are not analyzed further.

Dorsolateral fold condition: There is relatively little variation in this character and the variation that exists is difficult to evaluate in terms of the impact preservation has on recognition of fold condition. Most individuals have no dorsolateral folds. In a few individuals, a short ridge or elongated warts lie in the dorsolateral fold region posterior to the eye. The variation in this character is not analyzed further.

Male secondary sexual characters: All males lack secondary sexual characters of thumb or chest pads or spines or male arm hypertrophy as found in *Leptodactylus*.

Male vocal sac: Variation in this character is minimal and difficult to evaluate in terms of preservation artifact. In most males, the vocal sac is single and internal; in a few males, the single vocal sac has external indications of weak lateral folds. Variation of this character is not analyzed further.

Textures: Data were taken on textures of the dorsum, the upper shank, the outer tarsus, and sole of foot. In all cases the degree of development of shagreen and tubercles was difficult to categorize consistently and differentiate from preservation artifact. The

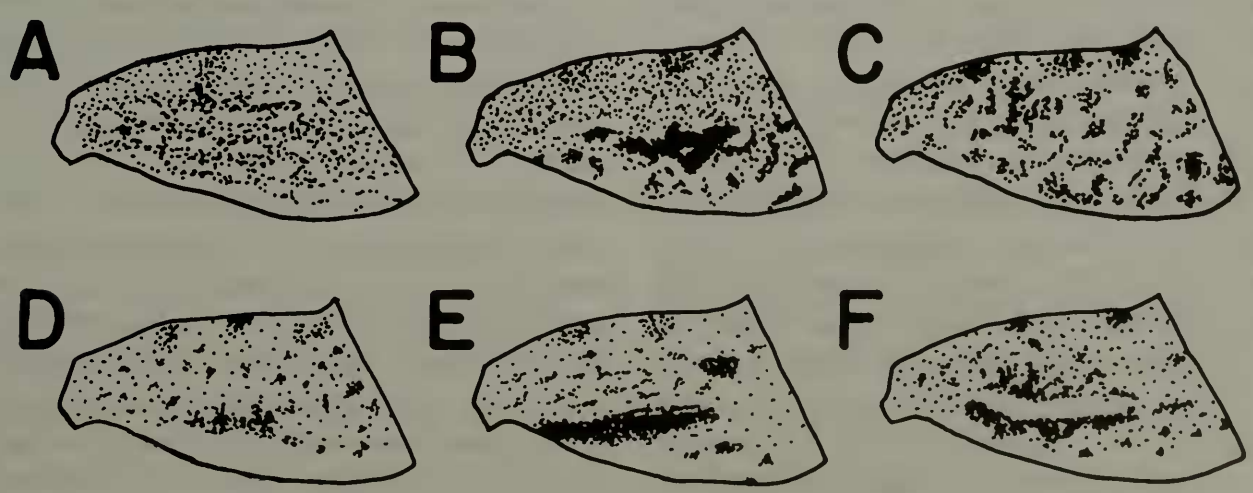

Fig. 5. Posterior thigh pattern standards.

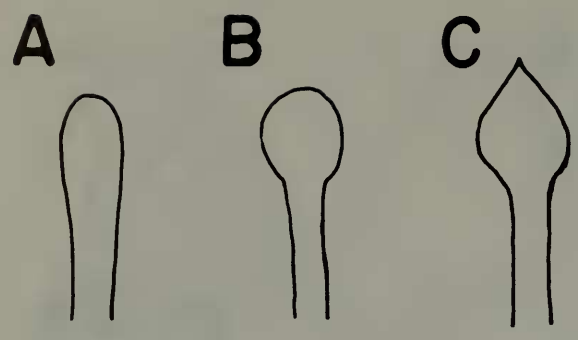

Fig. 6. Digit tip dorsal outline standards.

dorsum is tuberculate, with either small black-tipped or white-tipped tubercles, usually more densely packed posteriorly. The dorsum may also be somewhat granular, have a shagreen, or be smooth. The upper shank and outer tarsus consistently have tubercles, black and/or white tipped, and the surfaces may also be shagreened. The foot is either smooth or the outer margin has a few black/white tipped tubercles and/or a shagreen. Variation for these characters is not analyzed further.

Finger tip dorsal outline: For both finger and toe tip shapes, the outline shapes standardized by Savage (1987) for *Eleutherodactylus* were used. For both finger and toe tip dorsal outlines, only three of Savage's (1987) shapes were encountered corresponding to his unexpanded even (Fig. 6A), expanded even (Fig. 6B), and expanded pointed or lanceolate (Fig. 6C) states. The third finger tip is the most expanded and is the digit from which data were taken. Very little variation was encountered, suggesting that observer variation in interpreting shape was probably as large as actual variation. The conditions recorded ranged from not expanded, just A, A, A-B, or A-C. Variation is not analyzed further for this character.

Toe tip dorsal outline: The same standards were used for toe tips as for finger tips (Fig. 6). Data were recorded for both the third and fourth toe tips. The conditions for the third and fourth toe dorsal outlines are very similar. For 165 individuals, the conditions are identical, for 9 individuals the fourth toe dorsal outline is perceptibly more expanded than for the third, and for 75 individuals, the third toe dorsal outline is perceptibly more expanded than the fourth. As the third toe tip is a bit more expanded in the total sample, data are analyzed only for the third toe tip.

Dorsal toe grooves: The dorsal surfaces of the toes typically have from 2–5 grooves involving the epidermis and dermis. The grooves are almost parallel to each other along the long axis of the toe, but radiate slightly outward from the proximal toe tip to the distal tip. Usually the grooves extend almost the entire length of the expanded portion of the toe tip, but the grooves do not reach the tip of the toe. Counting the exact number of grooves is not always precise as the grooves are sometimes incomplete and preservation artifact can obscure the definition of the grooves. Data were taken for both the third and fourth toes. As for the dorsal outline, the conditions within individuals are similar, but typically the third toe has one more groove than the fourth. For 96 individuals, the third and fourth toes have the same number of grooves, for 18 individuals, the fourth toe has more grooves than the third, and for 132 individuals the third toe has more grooves than the fourth. Because the raw data indicate that the variation in the fourth toe mirrors that seen in the third, only the data for the third toe are analyzed further.

Analysis of preceding characters: The preceding characters are recorded as discrete entities even though variation is mainly continuous. Because the data are discrete, chi-square analyses are used to determine whether occurrence frequencies of states differ significantly. The 0.05 convention is used to determine significance. Data were adjusted, when necessary, to reach a minimum cell size of an average expected frequency of 5 (Hayek 1994:239). Data were first examined to determine whether states for adult males and females differed significantly. If they did not, then data recorded for juveniles were added to both the male and female data to provide more robust data sets for statistical analysis among geograph-

ic regions (see definitions of regions below).

Measurement data and analyses.—Measurements were taken on the following variables, as defined by Gascon et al. (1996): snout-vent length (SVL), nostril separation, eye width anterior, eye width posterior, head width, head length, eye to nostril distance, thigh length (=femur length of Gascon et al. 1996), shank length (=tibia length of Gascon et al. 1996), foot length, tympanum diameter (=tympanum height of Gascon et al. 1996), eye length, maximum width of third finger, and maximum width of fourth toe. Measurements were taken with a Helios dial calipers and recorded to the nearest 0.1 mm.

Only adult specimens are used for the measurement data analyses. As males and females are sexually dimorphic in size, they are analyzed separately (L. C. Hayek, C. Gascon, and W. R. Heyer (unpublished data) discuss multivariate analyses on morphometric data on *Vanzolinius.*) The data are analyzed using the software program SYSTAT 5 (Wilkinson et al. 1992).

Larval data.—To my knowledge, the only larvae available are those reported on by Duellman (1978) from a single locality in Ecuador (Mera, Pastaza). Specimens KU 121362–121363 are larvae ranging from Gosner stages 30–38. Specimens KU 121360–121361 are just metamorphosed individuals. There is no internal evidence from study of these specimens to either establish that they are *Vanzolinius* or they are not. Dr. John Lynch collected the specimens and informs me (pers. comm.) after he consulted his field notes, " . . . it appears that I guessed on the identification . . . on the basis of habitat selection. Hence, don't trust the identification." As nothing can be determined about geographic variation based on these specimens (even assuming they are *Vanzolinius discodactylus*), larvae are not treated further in this paper.

Advertisement call data and analyses.—Recordings of single individuals from five localities are available for analysis.

Brazil: Acre; Nova Vida, Rio Juruá, USNM Tape 256 Cut 12. Recorded at 1900 h on 17 March 1992 by Claude Gascon at a temperature of 25°C, no voucher specimen.

Brazil: Amazonas; Altamira, Rio Juruá, USNM Tape 255 Cut 2. Recorded at 1915 h on 17 November 1991 by Claude Gascon at a temperature of 25°C, voucher INPA 5021.

Brazil: Amazonas; Barro Vermelho, Rio Juruá, USNM Tape 254 Cut 5. Recorded at 1900 h on 27 October 1991 by Claude Gascon at a temperature of 24.4°C, voucher INPA 3352.

Brazil: Amazonas; Jainú, Rio Juruá, USNM Tape 254 Cut 13. Recorded at 1740 h on 2 November 1991 by Claude Gascon at a temperature of 26.1°C, no voucher specimen.

Ecuador: Napo; Limoncocha, USNM Tape 18 Cut 1. Recorded at 2000–2034 h on 9 July 1971 by Ronald Heyer at an air temperature of 23.4°C, water temperature 23.6°C, voucher LACM 92001.

Calls were analyzed using Canary 1.2 software (Charif et al. 1995) on a Power Macintosh 8500 computer. Calls were digitized for analysis at a sample rate of 22050 Hz and a sample size of 16 bits. Call rate was determined directly from recordings for periods ranging from 45 to 180 s per recording. Other call parameters were taken from a combination of waveform, audiospectrogram (=spectrogram as used in Canary manual), and spectrum analyses based on ten calls for each individual. Most of the recordings had considerable noise. Many parameters were taken from filtered calls. The filter around option was used for determining some parameters for USNM Tape 256 Cut 12 (filtered around 520–5000 Hz), USNM Tape 255 Cut 2 (filtered around 500–5000 Hz), USNM Tape 254 Cut 5 (filtered around 330–4000 Hz), and USNM Tape 18 Cut 1 (filtered around 500–4500 Hz).

Definition of geographic areas for analysis.—The primary purpose of this study is

to determine the nature of geographic variation found within *Vanzolinius discodactylus*. Sample sizes are insufficient to analyze the data from each locality independently. Localities were plotted on a map and localities were grouped on the basis of geographic proximity (Fig. 7). The rationale used for grouping localities involved trying to maximize three criteria simultaneously: to have as many groups as possible in order to characterize geographic variation; to have as many individuals as possible in each group to permit robust statistical analyses; and to maintain geographic integrity. With respect to geographic integrity, a rule of thumb of keeping localities within the same major river drainage basins was generally applied (Areas A, B, C, D, F, G, H), but not exclusively so (Area E). Initially 10 geographic area groupings were made. When the data were examined for these groupings to see if they were sufficient, three of the groups lacked sufficient data for analysis. Two Colombian localities were sufficiently isolated from each other as well as other samples to be placed in their own groups; unfortunately, the specimens from both localities are faded such that data are incomplete for them. Thus, data for the Colombian localities of Caldas; Villa María and Caquetá; Florencia, are not included in the geographic analyses (Fig. 7, upper two squares). A single Peruvian locality (Ucayali, Yarinacocha) also formed a distinct geographic group by itself and contains one faded specimen, unsuitable for further geographic analysis (Fig. 7, lower square). Eight geographic groupings remain and are identified by letter in further discussion: (A) northern Amazonian Ecuador; (B) southern Amazonian Ecuador; (C) Amazonian Peru; (D) the Brazil-Colombia border region; (E) easternmost known localities for *Vanzolinius* in Amazonian Brazil; (F) the mid-region of the Rio Juruá of Brazil; (G) the upper region of the Rio Juruá in the Brazilian State of Amazonas; and (H) the upper region of the Rio Juruá in the Brazilian State of Acre.

As there are but five individuals available from Region D, (1 female, 1 male, 3 juveniles), Region D data are omitted from the analyses by areas, unless otherwise noted.

Results

Dorsal snout pattern.—This was the only character for which some individuals clearly demonstrated two states (this exception involved only conditions B and C both occurring in the same individual), suggesting partial independent genetic control of this character. The states (Appendix 2) were collapsed for analysis to three: (1) pure A, (2) any B, and (3) any C. Because several individuals had both states (2) and (3), the total number of state conditions analyzed exceeds the number of individuals examined for this character only.

The chi-square analysis by sex was not significant ($\chi^2 = 1.35$; $df = 2$; $P = 0.50 > 0.30$). Thus, male, female, and juvenile data were combined to analyze by geographic area. The chi-square analysis by geographic area is significant ($\chi^2 = 69.92$; $df = 12$; $P < 0.001$). In partitioning the results, regions A+B are distinct from regions E+F+G+H. Region C is not distinct from either of the other two area groupings.

Light postorbital eye stripe.—For individuals having different states on either side of the head, the more distinctive state was scored for statistical analysis (e.g., an individual recorded as having state (+) on one side of the head and + on the other was treated as having the + state for statistical analysis). The chi-square analysis by sex was significant ($\chi^2 = 6.43$; $df = 2$; $P = 0.05 > 0.02$); therefore the variation among geographic areas has to be analyzed separately by sex. For females, the chi-square analysis by geographic area is significant ($\chi^2 = 42.43$; $df = 12$; $P < 0.001$). In partitioning the significance, regions B+E are distinct from regions A+C+F+G+H. In order to meet the minimum expected cell size criterion for statistical robustness for males, the data had to be collapsed by rec-

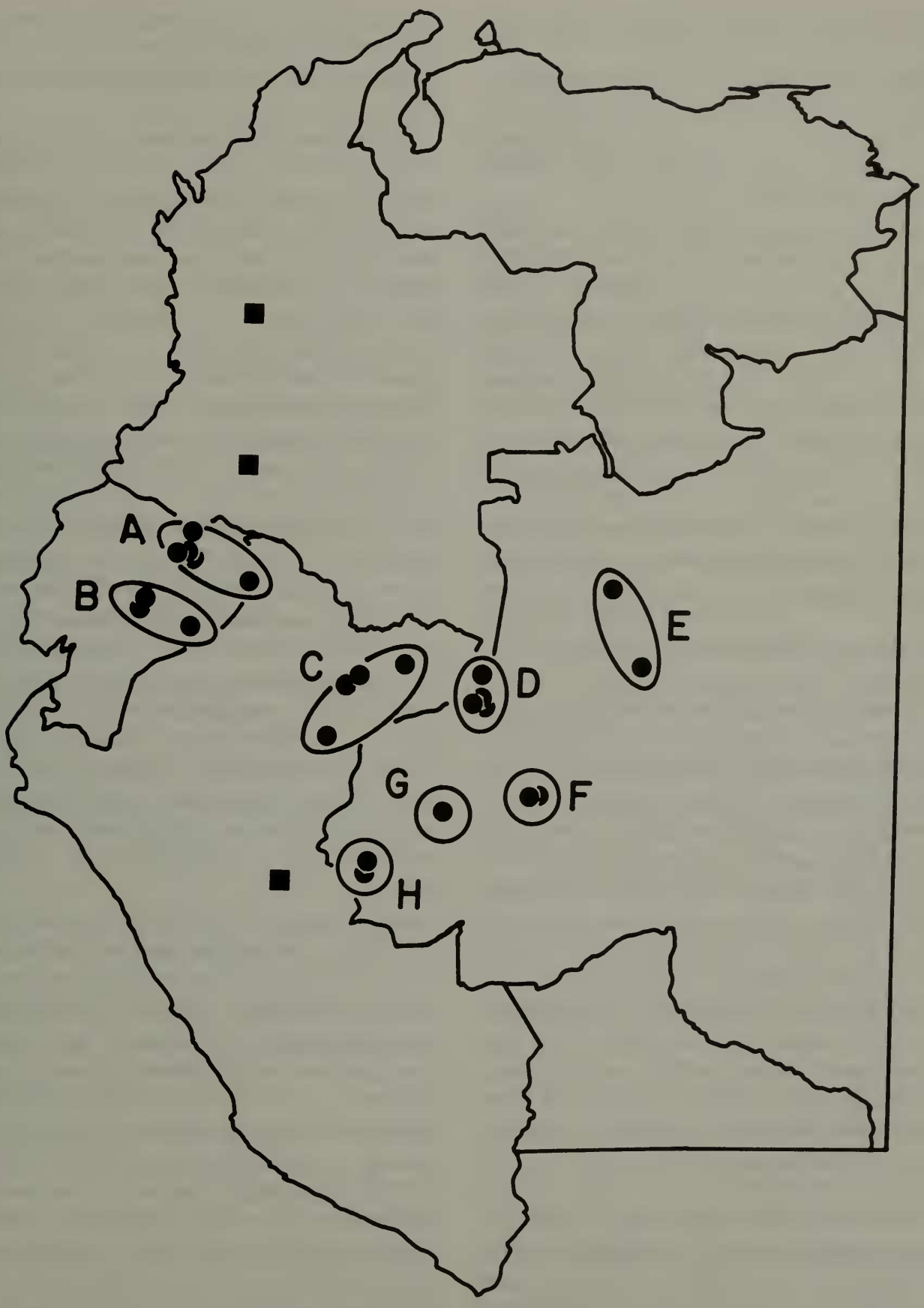

Fig. 7. Map of northwestern South America showing known distribution of *Vanzolinius discodactylus*. Guyana and Brazil are truncated by the 60°W meridian; Bolivia and Brazil by the 15°S parallel. Squares are single localities excluded from analysis of geographic variation. Circles and ellipses labelled A–H indicate groupings of localities (dots) used for analysis of geographic variation. A dot may represent more than one locality.

ognizing but two character states: absent (− state) or present (combined (+), +, +! states). The chi-square results are significant ($\chi^2 = 27.80$; $df = 6$; $P < 0.001$). In partitioning the results, the significance is due entirely to the distinctiveness of the Area B specimens.

Light subocular bar.—For individuals having different states on either side of the head, the more distinctive state was scored for statistical analyses. The chi-square analysis by sex was significant ($\chi^2 = 6.85$; $df = 2$; $P = 0.05 > 0.02$). In order to meet the assumption of minimum expected cell size for females, the data for Area H were deleted. The resultant chi-square analysis is not significant ($\chi^2 = 15.49$; $df = 10$; $P = 0.20 > 0.10$). To meet the minimum expected cell size for the male data, the states were collapsed to two: absent (− state) and present ((+) and + states). The resultant chi-square analysis is not significant ($\chi^2 = 9.59$; $df = 6$; $P = 0.20 > 0.10$).

Dorsal pattern.—For statistical analyses, the first state recorded for intermediate conditions is used (e.g., a specimen recorded as having condition A−B is scored as having condition A for the statistical tests). The chi-square analysis by sex is not significant ($\chi^2 = 2.93$; $df = 3$; $P = 0.50 > 0.30$); female, male, and juvenile data were combined to analyze by geographic area. To meet the assumption for minimum expected cell size, States D and D-1 are combined; however, Area D is included. The chi-square result among areas is significant ($\chi^2 = 203.09$; $df = 28$; $P < 0.001$). In partitioning the results the following area groupings are distinct from each other: A; B; C+D+E; F+G+H.

Dark mid-dorsal pin stripe.—The chi-square analysis by sex is significant ($\chi^2 = 5.86$; $df = 1$; $P = 0.02 > 0.01$). To meet the minimum expected cell size criterion for females by area, Area H was deleted. The chi-square result is significant ($\chi^2 = 11.47$; $df = 5$; $P = 0.05 > 0.02$). Partitioning the results indicates the following area groupings are distinct from each other: A+B; C+E+F+G. For males, the chi-square analysis of character states by area is not significant ($\chi^2 = 9.43$; $df = 6$; $P = 0.20 > 0.10$).

Throat and chest pattern.—As for dorsal pattern, the first state recorded for intermediate conditions is scored for the statistical analyses. State E was scored for only one individual and is not considered in the analyses. As only two known-sex individuals have State B-1, and only one known-sex individual has State C-1, State B-1 is combined with State B and State C-1 is combined with State C in the analyses. The chi-square analysis by sex is significant ($\chi^2 = 23.20$; $df = 4$; $P < 0.001$). To satisfy the minimum expected cell frequency assumption for females, drastic manipulations are required. Areas B and H are excluded. States A-1 and A are combined. The resultant chi-square analysis is significant ($\chi^2 = 23.39$; $df = 8$; $P = 0.01 > 0.001$). In partitioning the results, only areas E+F are distinct. Drastic manipulations are also required to analyze the male variation. States C and C-1 are deleted. Areas C, E, G, and H are deleted. States A-1 and A are combined. The resultant chi-square test is not significant ($\chi^2 = 1.90$; $df = 4$; $P = 0.90 > 0.50$).

Belly pattern.—As for dorsal pattern, the first state recorded for intermediate conditions is scored for statistical analyses. To meet the minimum expected cell frequency assumption for the analysis by sex, the following states are combined: A and A-1; B and B-1; C, C-1, and C-2; State D is deleted. The resultant chi-square analysis is significant ($\chi^2 = 8.60$; $df = 2$; $P = 0.02 > 0.01$). To analyze females, the same state combinations described above are used and Areas B and H are deleted to meet the minimum expected cell size assumption. The chi-square result is statistically significant ($\chi^2 = 56.20$; $df = 8$; $P < 0.001$). Partitioning the results indicates that the following area groupings are distinct from each other: A; C+E; F+G. To meet the minimum expected cell size assumption for males, only

the combined states (as above) from Areas B, E, and F could be analyzed. The chi-square results are significant ($\chi^2 = 24.43$; $df = 4$; $P = 0.001$); however, there are too few areas involved for meaningful partitioning.

Posterior thigh pattern.—As for dorsal pattern, the first state recorded for intermediate conditions is scored for statistical analyses. As only three individuals have State F!, it is combined with State F. The chi-square analysis by sex is not significant ($\chi^2 = 9.95$; $df = 5$; $P = 0.10 > 0.05$); females, males, and juveniles are combined to analyze character states by geographic areas. The chi-square analysis by area is significant ($\chi^2 = 101.30$; $df = 30$; $P < 0.001$). Partitioning the results indicates the following geographic area groupings are distinct from each other: A+B; C; E; F+G; H.

Third toe tip dorsal outline.—Only one individual was scored with any indication of State C, and it was an intermediate State B−C; for statistical analyses, that individual was scored as having State B. As only two individuals had the unexpanded state, that state is combined with the "Just A" State for analyses. The chi-square analysis by sex is not significant ($\chi^2 = 6.90$; $df = 4$; $P = 0.20 > 0.10$); females, males, and juveniles are combined for analysis of state frequencies among geographic areas. The chi-square analysis by area is significant ($\chi^2 = 158.78$; $df = 24$; $P < 0.001$). In partitioning the results, the following area groupings are distinct from each other: A; B+C; E; F+G+H.

Third toe tip dorsal grooves.—Because so few individuals had only one groove (Appendix 2), the individuals are combined with those having two grooves. The resulting chi-square analysis by sex is not significant ($\chi^2 = 0.58$; $df = 3$; $P = 0.80 > 0.70$); females, males, and juveniles are combined for analysis of state frequencies among geographic areas. The resultant chi-square analysis is significant ($\chi^2 = 34.90$; $df = 18$; $P = 0.01 > 0.001$). Partitioning the results indicates that the following geographic groupings are distinct from each other: C; E; A+B+F+G+H.

Measurements.—Because only two adult males represent Area G, they are deleted from the analyses.

MANOVA analyses were run on the two data sets (male and female). All univariate F tests were statistically significant ($P \leq 0.001$). The multivariate tests are also significant for both data sets (e.g., Wilks' Lambda for male data = 0.022, $F_{(70),\ 237} = 4.136$, $P < 0.001$; for female data Wilks' Lambda = 0.025, $F_{(84),\ 312} = 3.501$, $P < 0.001$). Thus, there is significant variation of the measurement data among the geographic areas.

In order to understand the nature of the geographic variation, discriminant function analyses were performed on untransformed data and are discussed separately for the male and female data.

The male data post-classification results (Table 1) indicate that sizes and shapes are distinctive for each area, with lesser distinctiveness in morphologies between Areas A and B. A plot of the first two canonical scores (Fig. 8) indicates that the Area A and B samples overlap each other to a greater extent than any of the other samples. The male measurement data support the following area groupings as distinct from each other: A+B; C; E; F; H.

The female data post-classification results (Table 2) also indicate that the morphologies are distinctive within each region, with less differentiation between Areas C and E and among Areas F, G, and H. The plot of the first two canonical scores (Fig. 9) demonstrates extensive overlap of specimen data for Areas C and E and Areas F, G, and H. The female measurement data indicate the following area groupings to be distinct from each other: A; B; C+E; F+G+H.

Comparison of the male and female data underscore that the males and females from Area C differ markedly in their association with the other samples. The Area C males are quite similar to those of Area H but dif-

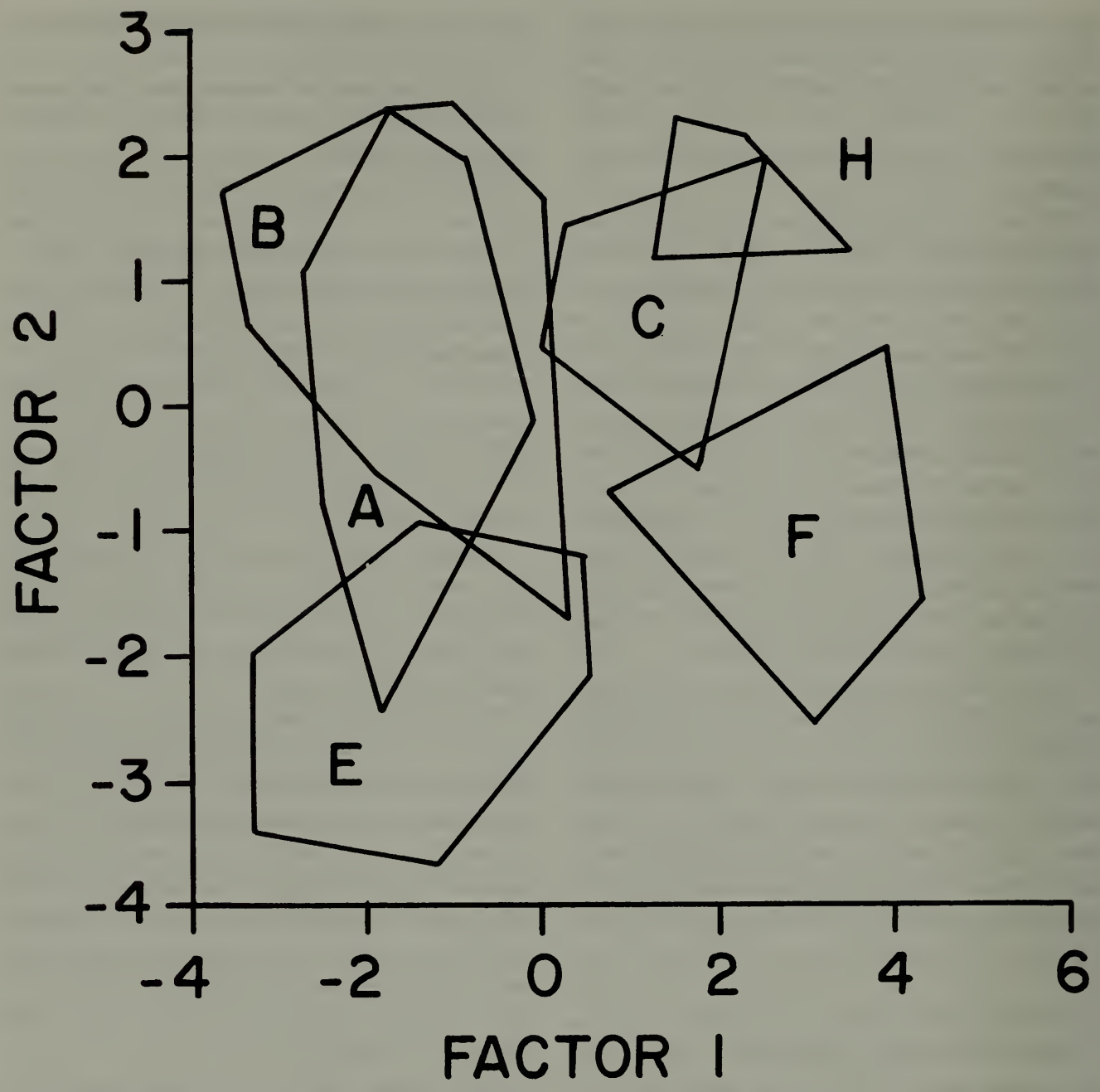

Fig. 8. Graph of first and second canonical factors for Area A–C, E–F, H males.

fer strikingly from those of Area E. Conversely, the Area C females are quite similar to those of Area E but distinct from those of Area H. These patterns suggest that size and shape have responded to separate selection pressures for males and females in *Vanzolinius.*

Advertisement calls.—The call from Limoncocha, Ecuador has been analyzed and described previously (Straughan & Heyer 1976).

Calls consist of individual notes which are partially pulsed. The basic call parameters are similar among all five recordings (Table 3). The exact durations of the calls are difficult to determine, as it appears that there is microphone ringing.

The most variation among calls involves: packaging of pulses; relative sharpness of attack; one or two distinct broadcast frequency bands; and maximum broadcast frequency energy. (The recording qualities are insufficient to adequately evaluate harmonic structure.) There is a continuum of variation from a note that has relatively weak partial pulses to a note that has a few strong pulses, almost or entirely complete, each of which may or may not be partially pulsed

Table 1.—Discriminant function analyses for male *Vanzolinius* measurement data by geographic areas.

	Number of observations classified into areas					
	A	B	C	E	F	H
Area A	5	2	0	1	0	0
Area B	1	18	0	1	0	0
Area C	0	0	9	0	0	1
Area E	0	0	0	12	0	0
Area F	0	0	0	0	12	0
Area H	0	0	0	0	0	6

Table 2.—Discriminant function analyses for female *Vanzolinius* measurement data by geographic areas.

	Number of observations classified into areas						
	A	B	C	E	F	G	H
Area A	7	0	0	0	0	0	0
Area B	0	4	0	0	0	0	0
Area C	0	0	5	1	0	0	0
Area E	1	0	5	22	0	0	0
Area F	0	0	1	0	14	1	4
Area G	0	0	0	0	0	5	2
Area H	0	0	0	0	0	1	2

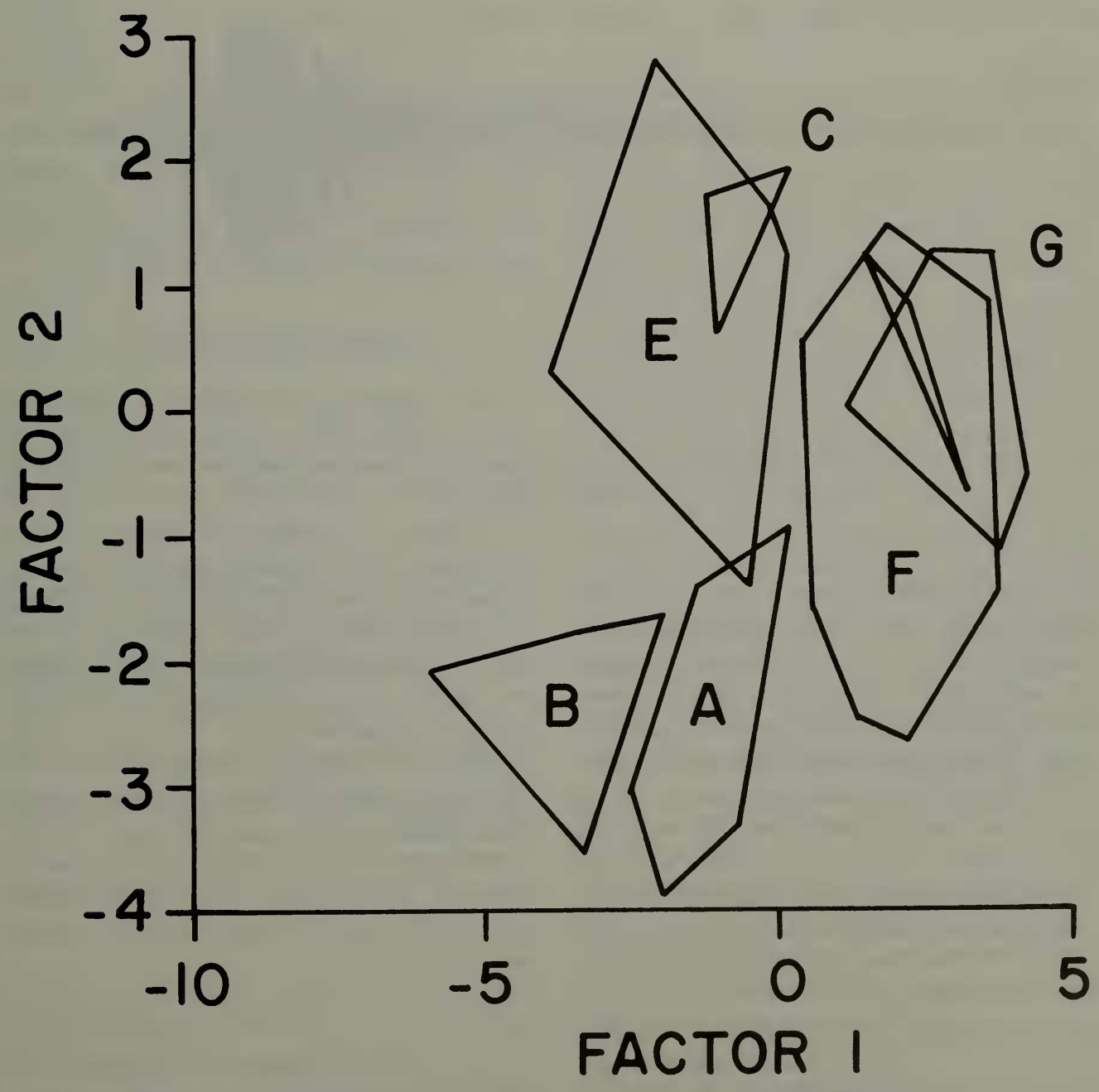

Fig. 9. Graph of first and second canonical factors for Area A–C, E–H females. The polygon for Area H is not labeled and occurs entirely within polygon F.

Table 3.—Advertisement call data for *Vanzolinius* specimens from five localities.

	Geographic area				
	A	F	F	F	H
USNM Tape & Cut	18,1	254,5	254,13	255,2	256,12
Call rate per s	0.8	1.1	1.3	1.4	0.9
Mean call duration (s)	0.14	0.14	0.12	0.13	0.14
Modal # of strong pulses	1	5	4	1	1
Mean # of total partial pulses	16.8	21.7	18.3	13.9	18.5
Very sharp attack	+(?)	—	—	+	+
Portion of call with most energy	First half to middle	First half to middle	Middle to first half	First half	First half
Two distinct broadcast bands	—	+	+	+	weak
Modal value of most intense frequency for lower broadcast band	—	1630	1560	1730	1980
Modal value of most intense frequency for higher broadcast band	2850	2570	2410	2590	2590
Modal values of total frequency range	2260–3190	1330–2930	1160–2830 1250–	1320–3020	1490–3010 –3090
Harmonics	—	—	weak	weak?	weak?

(Fig. 10). All calls are frequency modulated, increasing over a short time span. The relative sharpness of attack varies from moderate to sharp (Fig. 11). During the frequency rise at the beginning of the call, there is variation in how much energy is broadcast during the beginning of the call (1 or 2 broadcast bands, Fig. 12). The dominant frequencies of frog calls are known to vary with temperature, typically in an increasing manner (Duellman & Trueb 1986: 104). Although there is relatively little variation of environmental temperatures at times of recordings, the few data points suggest an inverse relationship with temperature with maximum broadcast frequency energy (Fig. 13). This, in turn, suggests that the variation in dominant frequencies is due to something other than temperature.

Given such small sample sizes, it is not clear how much of the observed variation among calls is due to individual variation versus population or regional differentiation. The recordings from the paired sites of Barro Vermelho and Jainú (see Gascon et al. 1996) share distinctive call features of pulse packaging and sharpness of attack; these features are not found in the other call from the same geographic area (F), Altamira. Thus, this call variation appears to be very local. Two other features vary among the geographic areas, the presence of one or two broadcast frequency bands and dominant broadcast frequencies (Table 3).

Differentiation Patterns

Color patterns, morphology, measurements, calls.—Two trends are apparent from the preceding results (summarized in Table 4).

1) There is a strong component of differentiation at the local geographic area as defined by Areas A–H in this study. There is a suggestion that local differentiation is more pronounced throughout the region covered by Areas A–E than for the region covered by Areas F–H.

2) There is also a component of geographically related differentiation. Areas A and B share a set of states; Areas C, (D), and E share a set of states (evidence for including D based on only one available character, however); and Areas F, G, and H also share a set of states.

The above characterizations are conservative. The actual levels of differentiation in *Vanzolinius* doubtless are greater than those demonstrated in this study. In many cases, insufficient sample sizes forced col-

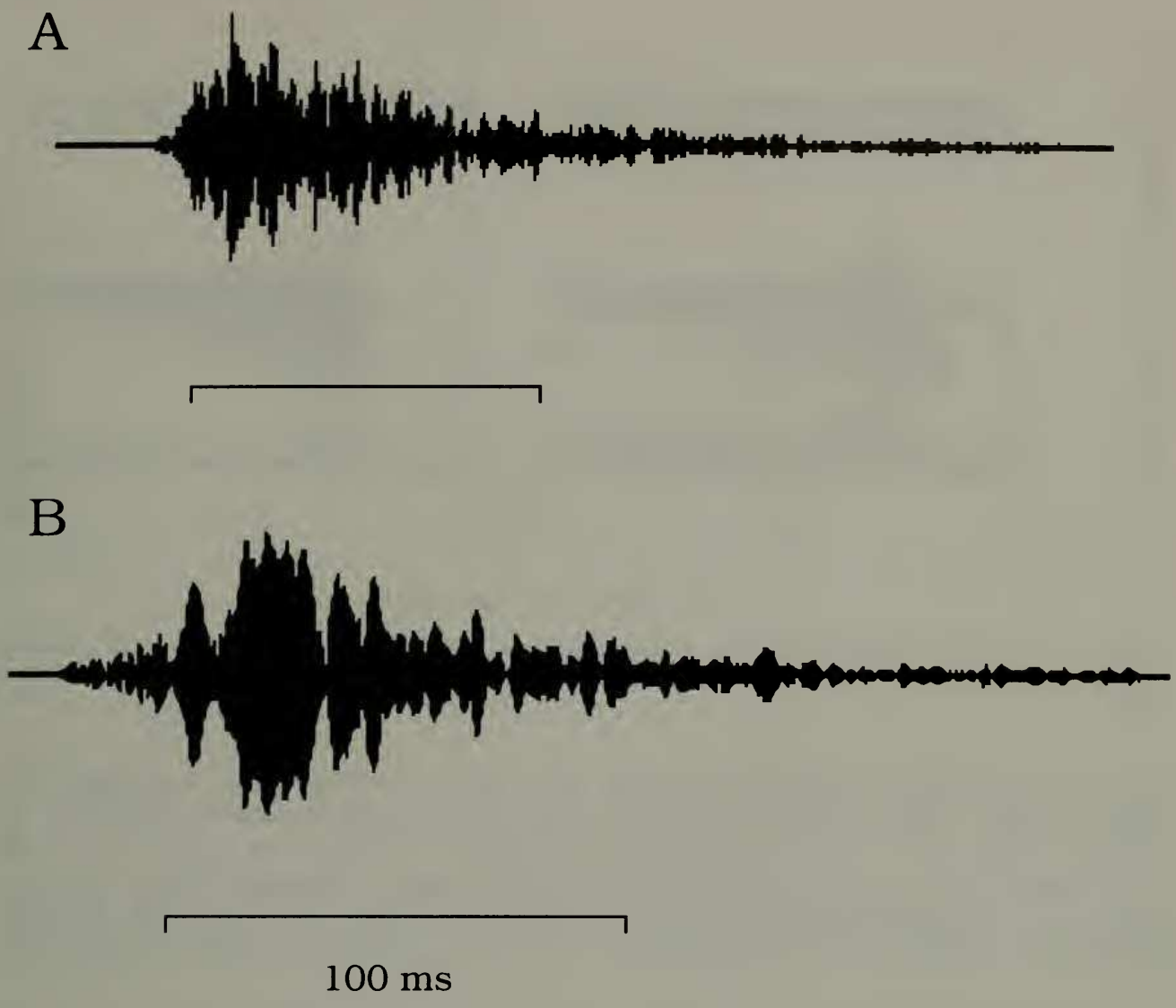

Fig. 10. *Vanzolinius* advertisement call, wave forms. A. Weakly pulsed call, USNM Tape 256, Cut 12. B. Strongly pulsed call, USNM Tape 254, Cut 5. (Both calls filtered.)

lapsing of either the extent of variation observed, deletion of geographic areas, or both during the statistical analyses. It is likely that larger sample sizes would reinforce the patterns described above and perhaps better delineate the patterns of differentiation among areas C-D-E and F-G-H.

Enzymes.—Gascon et al. (1996) published protein starch gel electrophoretic results for 20 presumptive loci for samples corresponding to Areas E, F, G, and H as defined in this study. Using their published data, the samples sizes for each geographic area are E = 41, F = 24, G = 13, and H = 2. Results using Nei's (1972) genetic distance values in a multidimensional scaling analysis (Wilkinson et al. 1992) indicate a general similarity to the morphologically and advertisement call based results. Each area shows some genetic-estimate differentiation (Fig. 14). There is not complete concordance of genetic-estimate differentiation with geography in that adjacent areas E and F are the most distinctive area pair in the data set (Fig. 14).

As indicated with advertisement call data, the actual area/population structure unit where differentiation occurs is at a finer scale than the size of the geographic areas A–H used to group samples for morphological and call analyses. In order to examine the effect of genetic-estimate differentiation among sites where sample

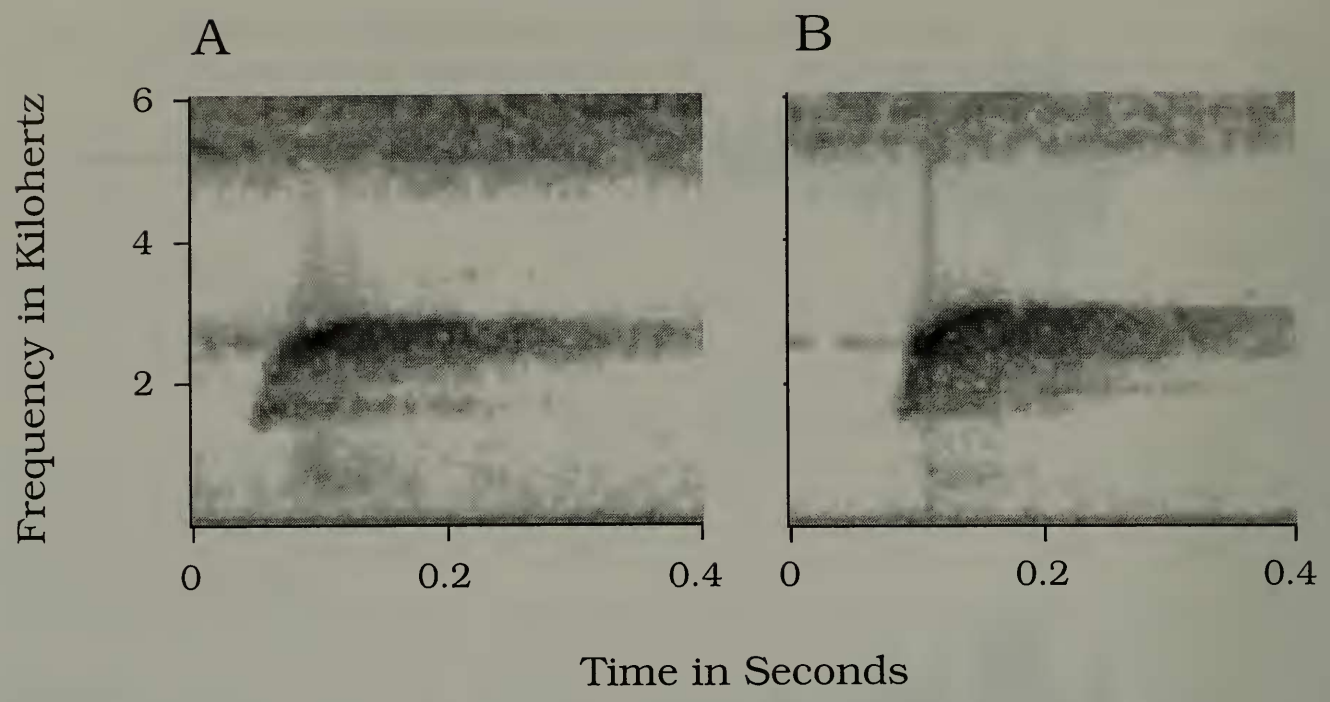

Fig. 11. *Vanzolinius* advertisement call, audiospectrograms. A. Sharp attack, USNM Tape 254, Cut 5. B. Very sharp attack, USNM Tape 256, Cut 12. (Neither call filtered.)

sizes were appropriate, all sites for which at least 5 individuals were available were analyzed using Nei's distances (1972) in a multidimensional scaling analysis (Wilkinson et al. 1992). The results indicate that there is differentiation among localities (Fig. 15, note however, that the separation on the y-axis is 1/10 that of the x-axis). As might be expected, one of the nearby pairs of localities from the same side of the river (Gascon et al. 1996, locality numbers 6 and 7, Fig. 1, Vira-Volta

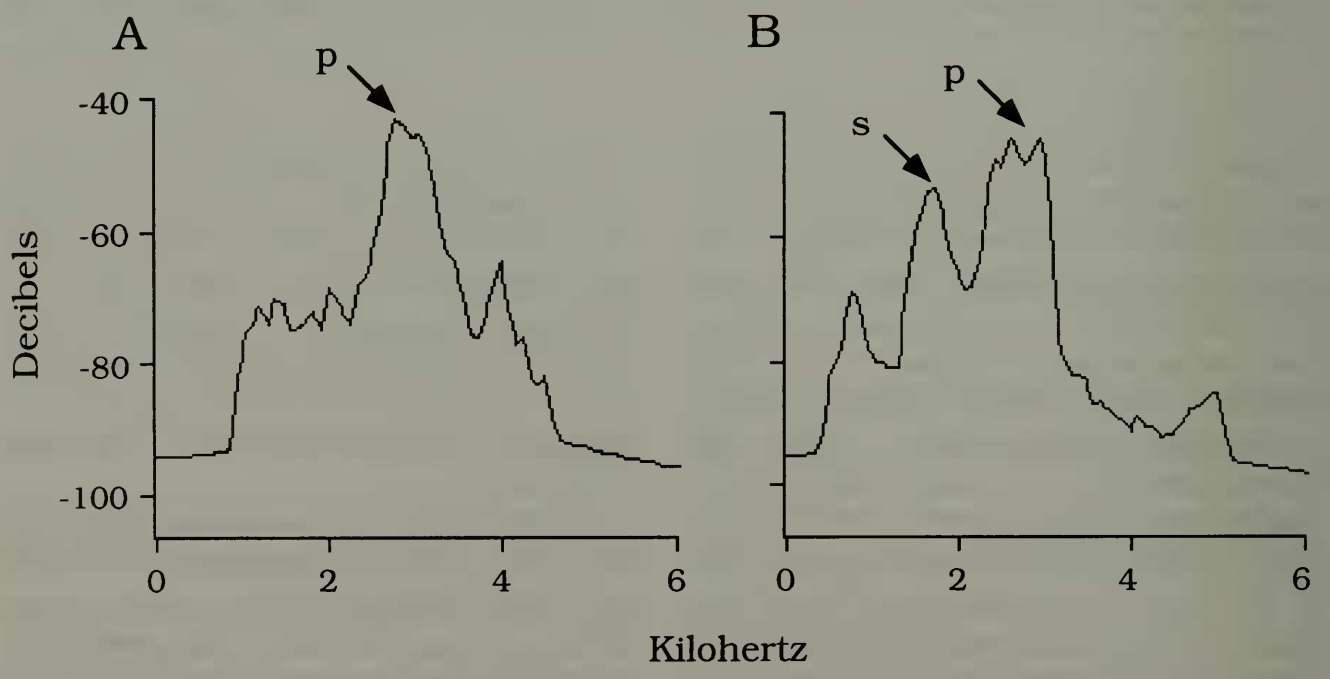

Fig. 12. *Vanzolinius* advertisement call, spectrum analyses. A. Call with virtually all of the broadcast energy in a single peak (p, maximum energy at 2750 Hz), USNM Tape 18, Cut 1. B. Call with significant energy in a second broadcast peak (primary peak, p, with maximum energy at 2590 and 2920 Hz, secondary peak, s, with maximum energy at 1700 Hz), USNM Tape 255, Cut 2. (Both calls filtered.)

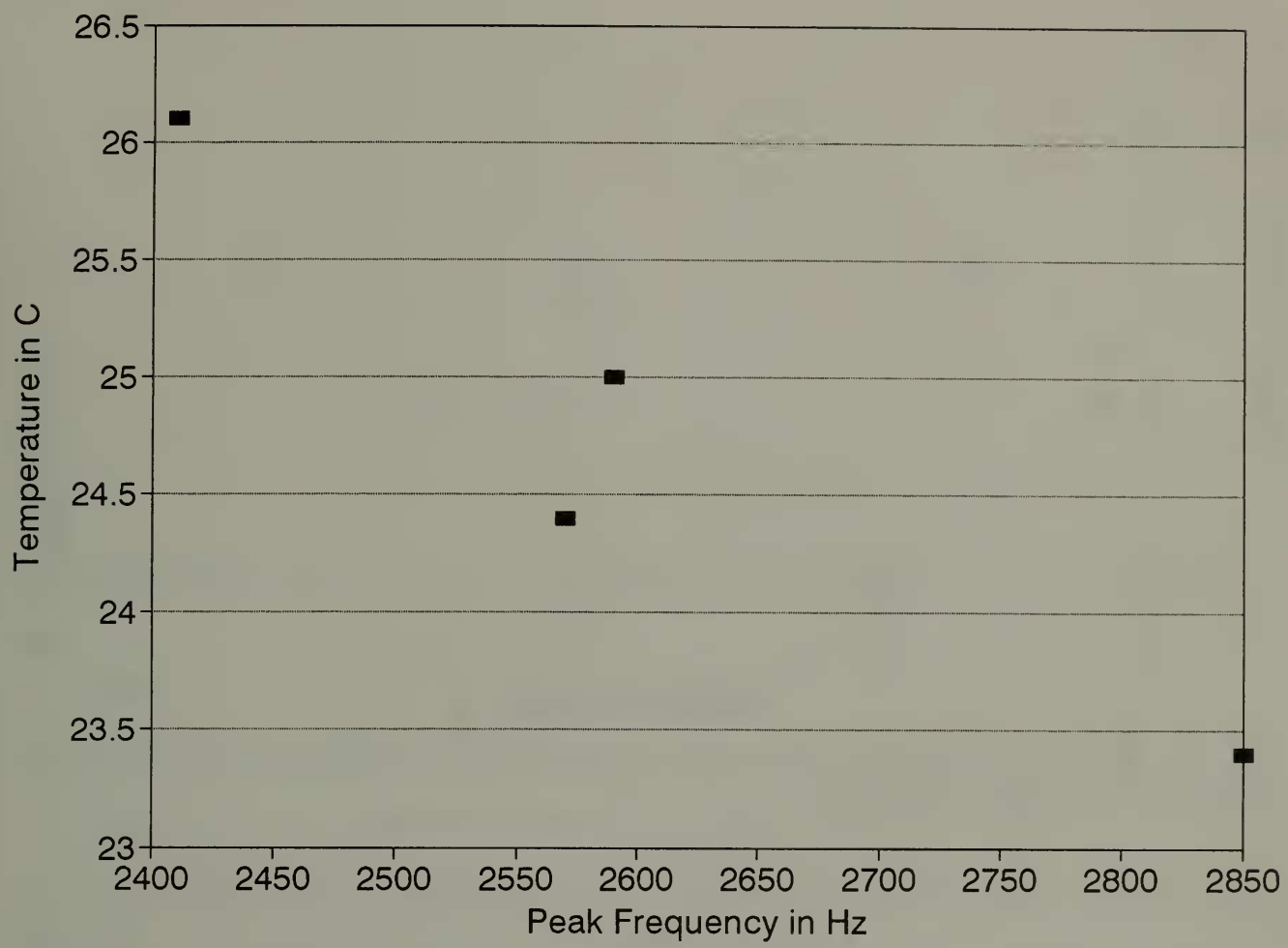

Fig. 13. Plot of temperature versus maximum broadcast energy in *Vanzolinius* calls.

varzea and terra firme sites) shows essentially no differentiation. However, the amount of differentiation between the other nearby pair of localities from the same side of the river (Gascon et al.'s locality numbers 10, Altamira and 11, Jainu (=Barro Vermelho), both varzea) are about as different from each other as any other pair of localities analyzed (Fig. 15). This distinctiveness is due to the Altamira sample. The pronounced genetic-estimate differentiation at this scale is unexpected. Such small-scale differentiation (in a geographic sense) results in an overall mosaic pattern of differentiation. Such a mosaic pattern of differentiation obfuscates any

Table 4.—Unique or shared character states among geographic area samples. Upper matrix with number of shared distinctive states. Diagonal with number of unique character states/total number of states analyzed. Lower matrix with total number of characters compared between areas.

	A	B	C	D	E	F	G	H
A	5/13	5	2			2	2	2
B	10	3/10	2		1	1	1	1
C	12	10	3/12	1	5	3	3	2
D	1	1	1	0/1	1			
E	12	10	12	1	4/12	3	2	1
F	13	10	12	1	12	1/13	9	7
G	11	9	11	1	11	11	0/11	6
H	10	9	9	1	9	10	8	2/10

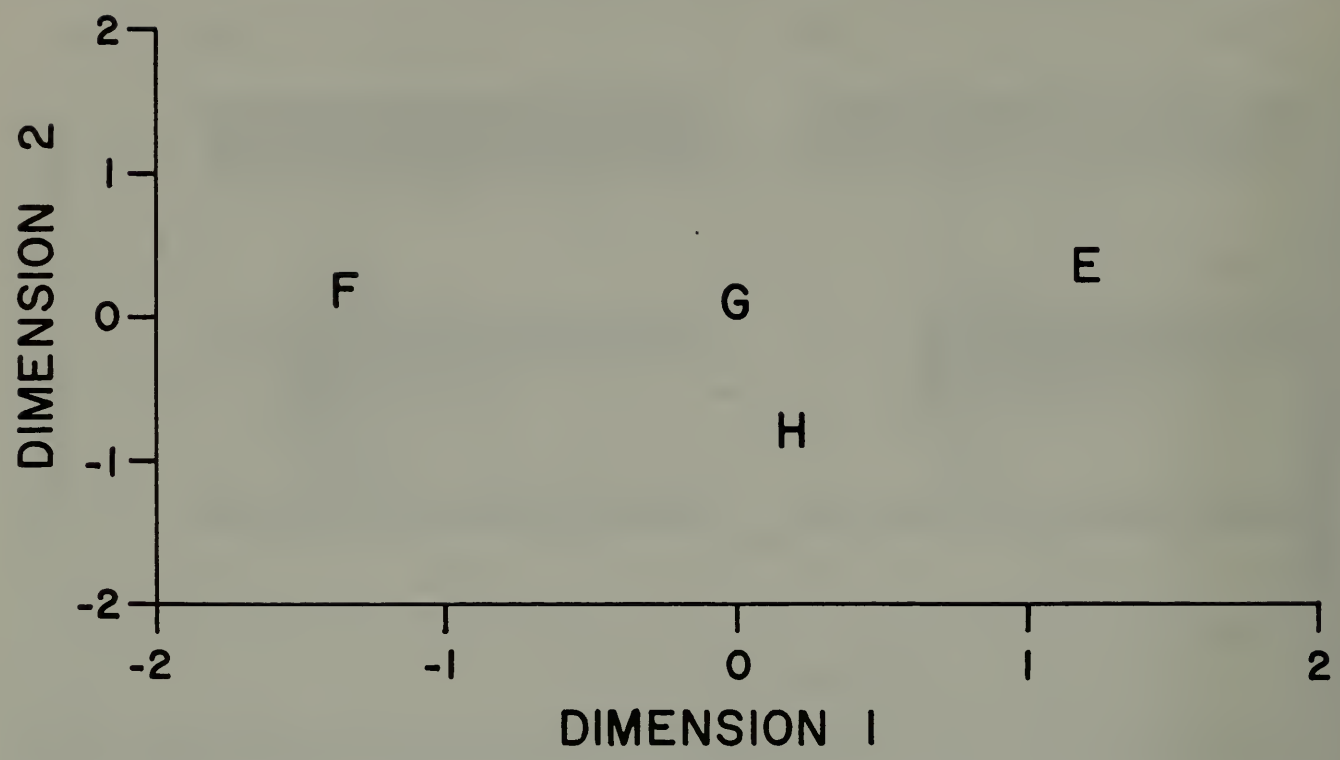

Fig. 14. Multidimensional scaling results for electrophoretic data given in Gascon et al. (1996), grouped by geographic areas as used in present study.

larger pattern of geographic differentiation.

The very local genetically based differentiation pattern provides corroboration and explanation of the results based on the morphological and advertisement call analyses presented previously.

Discussion

Distribution.—As indicated previously, specimens USNM 146971–146973 from Colombia: Caldas; Villa María are faded. I have no doubt that they are *Vanzolinius,* however. As seen from the distribution based on other known localities (Fig. 7), the interandean locality of Villa María is curious. The specimens were part of the collection donated to the Smithsonian by Hermano Niceforo María. The specimens were originally in the Museo La Salle collection as numbers 45, 45a, and 45b. Adjacent to these specimen records in the USNM catalogue ledger, Museo La Salle numbers 44, 44a, 44b, 44c, 44d, and 231 are also listed from the same locality. Dr. John Lynch identified the 44 series (USNM 146974–146978 respectively) as *Eleutherodactylus fitzingeri* and 231 (USNM 146979) as *Eleutherodactylus* sp. Lynch and Myers (1983) reported *E. fitzingeri* from Nicaragua through Panama, the Chocó of Colombia, and the interandean valleys of Colombia, but not from the Amazonian versant of the Andes in Colombia (see their Map 6, p. 535). Although Lynch & Myers (1983:560–561) do not include USNM 146974–146978 in their list of specimens examined, the locality of Villa María falls within the distribution described by them. Thus, some specimens from the La Salle collection from Villa María are geographically appropriate. In order to determine whether a transcription error had occurred in relation to the locality data for the *Vanzolinius* specimens (USNM 146971–146973), I asked Dr. Lynch who was in charge of the Museo La Salle herpetological collection in Bogotá. My intention was to determine the original catalogue entries for these specimens. Dr. Lynch (pers. comm.) informed me that the Director of the Mu-

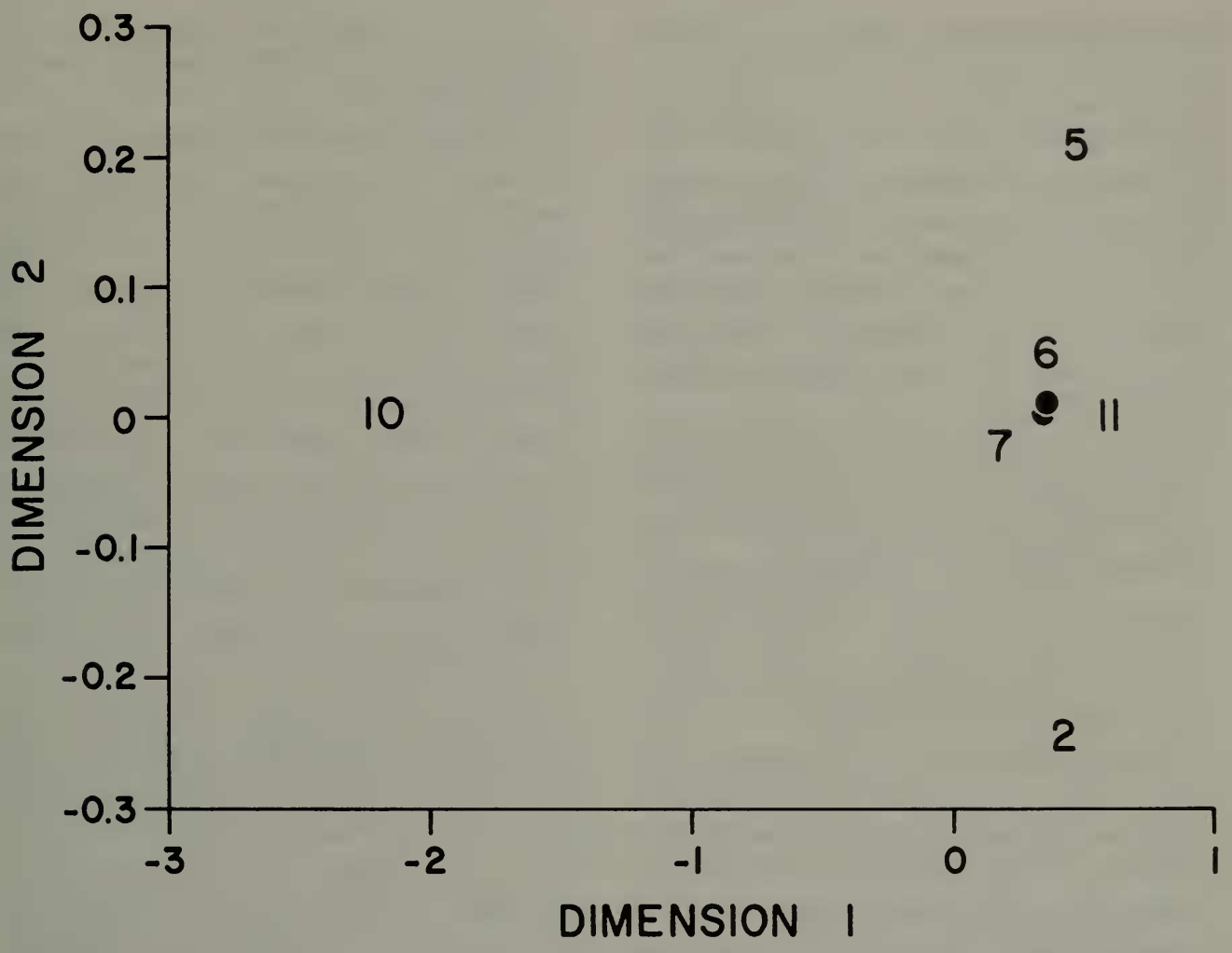

Fig. 15. Multidimensional scaling results for electrophoretic data given in Gascon et al. (1996), for individual localities represented by 5 or more specimen samples.

seo La Salle, in an effort to reduce duplicate information, had a student write new bottle labels for specimens in the herpetological collection and the Director discarded the original catalogues. Given the suspect nature of a species of amphibian with a western Amazonian distribution having a single disjunct population in an interandean Colombian valley, the locality of Villa María, Caldas, Colombia must be treated with extreme suspicion and not included in any distributional analyses until new collections verify the presence of *Vanzolinius* in Colombian interandean valleys.

Thirty six percent of the localities listed in Appendix 1 represent new locality records since 1990. The present patchy distribution (Fig. 7) certainly is due in part to collecting artifact. The current data indicate that the species has a distribution limited to western Amazonia. Exact knowledge of distributional limits of the species can only be approximated at this point, however. Sufficient collecting efforts have been undertaken in two critical areas for which absence data have some validity. *Vanzolinius discodactylus* has not been found in the Manaus, Brazil region, nor in the State of Madre de Dios, Peru. Thus the eastern and southern distributional limits likely fall between the currently known localities and Manaus and the Manú National Park.

Differentiation patterns.—Almost all studies of variation of the Amazonian herpetofauna have been directed at the species level. This is certainly appropriate, as

much work remains before the species limits of the Amazonian herpetofauna are well defined, particularly for amphibians.

A classic exception is the detailed study by Vanzolini and Williams (1970) on *Anolis chrysolepis,* where they studied geographic variation at the population level over the entire range of forms that had been associated with *A. chrysolepis.* A portion of their methods is pertinent to the present discussion (1970:25):

> The investigation of each character was begun by the joint consideration of 13 "major samples" and carried forward by the analysis of "transects"—series of localities more or less linearly arranged between major samples. In this manner a two dimensional differentiation pattern of each character was obtained.
>
> The organization of the major samples and transects was decided initially only on the basis of the materials available and of the geometry of a map of the area of study. The results of a first analysis were then used to adapt the methods to permit better clarification of the patterns perceived. For example, the evidence (in fact known beforehand but not taken into consideration in the first study) of the existence of a well differentiated form, previously believed to be a well set-off species, in the area from Surinam to eastern Pará, led to a preliminary arrangement of the Guianan and Guiano-Brasilian transects, and to their subsequent modification in order to show to better advantage the phenomena of transition between these populations and adjacent ones.
>
> This sort of feedback and even bias in the analysis is not only unavoidable but highly desirable in studies of geographical differentiation in South America. If we had a perfect network of localities, each one represented by good samples—with statistically sufficient numbers of males and females, and with all age classes represented—a system of isophenes would emerge from the analysis, which might even be computerized.
>
> In fact, the available collections are, as is usual with museum collections, not made for a specific purpose, an irregular and patchy representation of the group range, and the study must begin by the setting of preliminary hypotheses, to be tested. In our case the hypothesis is, in all instances, that differences between the major samples correspond to geographic patterns and not to mosaics, and this hypothesis must be tested by adaptations of the analysis to the materials available, to the numbers of specimens and their position on the map, in other words, by the consideration of transects.

Although the number of localities and samples for Amazonian amphibians and reptiles has certainly increased since 1970, the overall assessment as described by Vanzolini and Williams still holds true. The organization of current studies on differentiation patterns of Amazonian amphibians must still be decided on the basis of materials available and the geometry of a map of the study area. As a consequence, direct comparison of results among studies is not possible at present. However, the comparisons that can be drawn suggest some statements that can be tested for generality with additional studies.

Vanzolini & Williams (1970) found differences between samples from the geographic areas represented by the areas defined in this paper as A+B and C+D+F+G+H (see their map 8, p. 180). They also found that samples from the nearby localities of Limoncocha and Santa Cecilia, Ecuador differed in some characters (e.g., fourth toe lamellae in males, p. 38).

The only other study I am aware of that treats intraspecific geographic variation for an Amazonian amphibian that occurs in the same region with *Vanzolinius discodactylus* is that of Duellman and Mo-

rales (1990) for *Edalorhina perezi*. Duellman & Morales (1990) analyzed variation of dorsal texture and belly pattern of *E. perezi* by river drainage systems. Comparison of their map (fig. 1:21) with the geographic areas used in this study indicate coincidence of the following: Region A (this study) = Napo drainage samples (their study); Region B = Pastaza drainage samples; Regions C+D = Amazonas drainage samples. Their data (table 2:23) indicate the following: The Amazonas drainage and Napo drainage samples are similar for dorsal texture conditions, but both differ from the Pastaza drainage sample; the Napo and Pastaza drainage samples are similar for ventral pattern condition and differ from the Amazonas drainage samples. Thus the two characters they analyzed in detail show independent patterns of variation and both demonstrate patterns of differentiation at the regional level.

Anolis chrysolepis, Edalorhina perezi, and *Vanzolinius discodactylus* are all forest denizens within Amazonia. All three taxa demonstrate some level of geographic differentiation at rather restricted regional levels. Much of the variation is difficult to put in a broad geographic context in all three species studies, however, suggesting a strong differentiation at the very local level which results in a mosaic pattern of differentiation that tends to obfuscate any larger scale geographic patterns. This is underscored by the genetic estimate data available for *Vanzolinius*. Rather than eschew the null hypothesis of differentiation being a mosaic, rather than having a geographic basis as implied by Vanzolini & Williams (1970:25), perhaps we need to embrace the mosaic concept.

One avenue that needs exploration is to determine the lower spatial limits of differentiation. At present, all we can say is that differentiation occurs at the geographic level that collectors have traditionally used to define distinct, but nearby, collecting localities. Does differentiation occur at even a finer scale than that for forest associated Amazonian amphibians?

Prognosis for further studies.—The corroboration of results from studies of differentiation of *Vanzolinius discodactylus* based on morphological features and on genetic estimate data is most encouraging. We should be able to undertake strictly morphological analyses of other taxa of forest associated Amazonian amphibians with confidence that the resultant patterns of differentiation reflect evolutionary processes and are not strictly phenotypic responses to localized environmental conditions.

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Appendix 1. Specimens examined.

Geographic area assignments in parentheses.

BRAZIL. *Acre:* Nova Vida, (H), INPA 4490; Porongaba, (H), INPA 4271, 4287, 4291, 4294, 4296, 4350–4351; Porto Walter, (H), MZUSP 51574–51575; Sobral, (H), INPA 4348. *Amazonas:* Altamira, (F), INPA 3571–3573, 3584–3585, 3649, 3651, 5010, 5021, 5051, 5060, 5062–5063, 5103, 5132, 5166, 5173, 5177–5178, 5214, 5217–5218; Barro Vermelho, (F), INPA 3076, 3092, 3109, 3154, 3161, 3163, 3177–3178, 3198, 3229, 3352, 3385, 3387, 3397, 3399, 3405, 3411, 3454, 3507; Benjamin Constant, (D) CAS--SU 11835; Condor, (G), INPA 2573, 2587, 2608, 2640, 2642, 2644, 2883, 2904–2905, 2912, 2919–2921; Igarapé Tucuxi, Auati-Paraná, (E), MZUSP 28124; Nova Empreza, (G), INPA 2371, 2373, 2388, 2433, 2503; Nova Olinda, (F), INPA 3041; Parana (near Penedo), (G), INPA 2291, 2399; Penedo, (G), INPA 2410–2412, 2514; Rio Itacoaí, (D), MZUSP 9810; Vira-Volta, (E), INPA 5694, 5696–5703, 5720, 5727–5728, 5730, 5732, 5735–5737, 5757, 5761, 5763, 5766–5767, 5790, 5797–5803, USNM 348954–348983.

COLOMBIA. *Amazonas:* Leticia, left margin of Río Loreto Yacu (D), ICNMNH 11274; headwaters of Río Caiwima, ca 70 km NNE Puerto Nariño, (D), MCZ 97025, 97033. *Caldas:* Villa María (not assigned to area), USNM 146971–146973. *Caquetá:* Florencia (not assigned to area), USNM 147036–147037.

ECUADOR. *Napo:* Coca, 290–320 m, (A), KU 158609, 175463–175464; near Laguna Taracoa, 30 km downriver from Coca, ca 250 m, (A), MCZ 94884–94885, MZUSP 56380; Payamino, (A), USNM 196882; Río Yasuní (150 km upstream from Río Napo) (A), KU 175132–175133; Santa Cecilia, 340 m, (A), KU 104666, 109163, 111403, 111424, 111429, 119347, 119350, 126241–126242, 143518, 149295–149308, 152396, 175460. *Pastaza:* Mera, 1140 m, (B), KU 119303–119318, 178274–178282; Montalvo, 250 m, (B), RMNH 23990; Puyo and environs, (B), KU 119319–119322, 202647–202648, MCZ 90385, USNM 196878–196881, 343426–343427; Shell Mera (B), KU 99069, 99081–99082, 99085, 99090.

PERU. *Loreto:* Aldeia dos Indios Bora, 2 km N mouth of Zumun, (C), MZUSP 54189–54191; Estirón, Río Ampiyaco (C), AMNH 115691, MZUSP 23083, 24006, 24782–24786, 24793, 24797, 24803–24804, 24810, 24814, 24816, 24825; Moropon, (C), TCWC 41484; Requena, Jenaro Herrera, 140 m, (C), LR 4382 (to be deposited in Museo de Historia Natural, Universidad Nacional Mayor de San Marcos); Yanamona, (C), TCWC 41739. *Ucayali:* Yarinacocha, Río Ucayali, (not assigned to area), FMNH 56285.

Appendix 2. Color patterns and morphological data state distribution by sex among geographic areas.

Character	Sex	State	Geographic Area							
			A	B	C	D	E	F	G	H
Dorsal Snout Pattern	♀	A	6	6	3	1	7	2	3	1
		A-B		1	1		2			
		B-A								
		B	2	1	2		3	2		1
		B-C					2		1	1
		C-B	1				2	3	5	
		C	1	1	2		12	15	4	
		A-C					7		1	
		C-A			1		5	1		1
	♂	A	4	13	3		1	4		
		A-B	2	2	2		1			1
		B-A		1						1
		B	1	3	1		1	1		
		B-C	1			1			1	1
		C-B	1				3	1	1	1
		C	2	1	2		7	6	4	1
		A-C		2	2		1	1		
		C-A	1					1	1	1
	J	A	8	12	2	1	2	2		
		A-B								
		B-A	1							
		B	1							
		B-C					1		2	
		C-B	1				1			
		C	1	2		1	2	3	1	
		A-C	1	1		1				1
		C-A					1			

Light Postorbital Eye Stripe	♀	-	3	6	1		22	1	1	
		(+)	5	1	2	1	13	8	5	1
		+	2	1	6		5	14	8	3
		+!								
	♂	-	1	11			2			
		(+)	6	6	1	1	8	5	3	1
		+	5	4	6	1	3	9	5	5
		+!			3		1			
	J	-	5	14		2	2			
		(+)	7	1	2		3	3	1	1
		+	1				2	2	1	
		+!								
Light Subocular Bar	♀	-	2	4	2	1	23	9	5	1
		(+)	5	3	2		14	8	6	1
		+	3	1	5		3	6	3	2
	♂	-	1	10	1		5	3	2	
		(+)	6	7	1	2	7	6	5	1
		+	5	5	5		2	5	1	5
	J	-	5	7		1	4	3		
		(+)	5	7	2	1	2	2	2	1
		+	3		3		1			
Dorsal Pattern	♀	A	5	1	7	1	38	16	12	2
		B	1	1	1		2	4	2	2
		C	2	1				2		
		C-1	2							
		D		4						
		D-1		1						

	♂	A	8	11	9	1	14	7	6	5
		B	1					4	2	1
		C	1	1	1			2		
		C-1	2							
		D								
		D-1		9						
	J	A	6	3	2	3	6	7	1	1
		B	1				1		1	
		C	1	2						
		C-1	5							
		D		4						
		D-1		6						
Dark Mid-Dorsal Pin Stripe	♀	-	6	6	3	1	10	7	3	2
		+	4	2	5		30	15	11	2
	♂	-	8	12	7	1	5	5	2	5
		+	4	9	3		9	9	5	1
	J	-	8	6	1	1	1	2	1	1
		+	5	9	1	2	6	4	2	
Throat & Chest Pattern	♀	A	7	4			5	9	10	3
		A-1			3		16	7	3	
		B	2	3	6		8	4	1	1
		B-1				1				
		C					11	3		
		C-1								
		D	1	1						
		E								
	♂	A	5	7	4	1	2	2	5	2
		A-1	1				2	4		

		B	2	6	5		4	3	3	2
		B-1						1		
		C			1		5	1		1
		C-1								1
		D	3	8			1	3		
		E	1							
	J	A	9	10	1			4	1	1
		A-1	2	4	1	1	5			
		B	2			1	1	1	1	
		B-1								
		C		1			1			
		C-1								
		D								
		E								
Belly Pattern	♀	A	1		2		4	20	7	1
		A-1			1		6	1	4	
		B	2				13			1
		B-1		4	6	1	12			
		C	1				2	2	3	2
		C-1		1			3			
		C-2	4	3						
		D	2							
	♂	A		1		1	2	8	4	2
		A-1		3			1	4	1	
		B	2	1	2		4			
		B-1	1	6	3		4	1		
		C			2		3		3	4
		C-1	3	2	3					
		C-2	4	8						
		D	2							
	J	A					2	4	2	

		A-1		6		1	3			
		B	1		1					1
		B-1		4	1	1	1	1		
		C	1				1	1		
		C-1	2							
		C-2	6	5						
		D	3							
Posterior Thigh Pattern	♀	A	2	3	1		1		2	1
		B	2		1	1	12	7	1	1
		C	3	3			1	3	2	2
		D	2	1			5	6	7	
		E	1		4		19	5	2	
		F		1	2		1	2		
		F!			1		1			
	♂	A	1	5			1		2	3
		B	5	7	5		6	3	3	2
		C	4	4				3		1
		D	1	4		1	3	5	2	
		E	1		2		4	3	1	
		F			3					
		F!		1						
	J	A	5	3	1	2		1		1
		B		1			1			
		C	2	1		1				
		D	3	8			1	3		
		E	2	2	1		3	1	2	
		F	1				2			
		F!								
Third Toe Tip Dorsal Outline	♀	N.E.+		2						

		A	6	3	4		7			
		A-B	2	3	4		19	6	6	
		B-A					11	11	7	2
		B	2		1	1	3	6	1	2
	♂	N.E.+		4	1					
		A	8	11	3		1			
		A-B	2	4	4	1	9	6	3	4
		B-A		2			2	6	4	
		B	2		2		2	2	1	2
	J	N.E.+	1	6	1					
		A	9	7						
		A-B	1	2	1	1	2		1	
		B-A	2				3	4	1	1
		B				1	2	1		
Third Toe Tip Dorsal Grooves	♀	1								
		2	1	2			7	3	2	
		3	4	2	2	1	27	13	6	2
		4	4	3	6		6	5	5	1
		5	1	1	1			2	1	1
	♂	1						1		
		2	2	5	1		5			1
		3	5	8	2	1	8	9	7	3
		4	3	6	5		1	4	1	2
		5	2	2	2					
	J	1			1	1				
		2	2	5		1	2	1		
		3	7	9			4	3	1	1
		4	4	1	1		1	1	1	
		5								